

## GENOTYPIC VARIATION IN THE PHACELIA STRICTIFLORA COMPLEX<sup>1</sup>

GEORGE W. GILLETT

The *Phacelia strictiflora* complex occurs from the Texas Gulf Coast to peripheral upland habitats of northeast Mexico, the Edwards Plateau, Oklahoma, Arkansas, Louisiana, Mississippi, and eastern Alabama. It embraces populations nominally included under *P. strictiflora* (Engelm. & Gray) A. Gray; and *P. patuliflora* (Engelm. & Gray) A. Gray; also a large number of intermediate populations. The two species of this complex were included in a recent biosystematic study of the *Cosmanthus* phacelias, in which a crossing program was completed with eight additional *Cosmanthus* phacelias (Gillett, in press). Constance (1949) recognized four varieties of *P. strictiflora* and two varieties of *P. patuliflora*. Material grown in this study would correspond more nearly to *P. strictiflora* var. *lundelliana* Constance and to *P. patuliflora* var. *patuliflora*. Recognition of the *P. strictiflora* complex as a distinct evolutionary line seems justified by genetic and morphological evidence presented earlier (op. cit.). The current objective is to present evidence that has an important bearing on the evolutionary relationship of the two species of the complex.

Both species of this complex are self-compatible outcrossers with nine pairs of chromosomes. Populations of *Phacelia patuliflora* occur on lowland habitats, very often on sandy alluvium near sea level along the coast, extending inland to central Texas. Its penetration inland centers along alluvial lowlands between the Colorado and Nueces Rivers. Its coastal distribution extends from the vicinity of Houston to the mouth of the Rio Grande, the southern populations showing considerable gradation to intermediate forms. On the other hand, *P. strictiflora* is a species of upland habitats and occurs over a wide expanse of territory from northeast Mexico to Oklahoma and eastern Alabama. It is highly variable and very often occurs as a weed in fallow fields, roadsides, and disturbed areas.

---

<sup>1</sup>Aided by grants from the National Science Foundation.



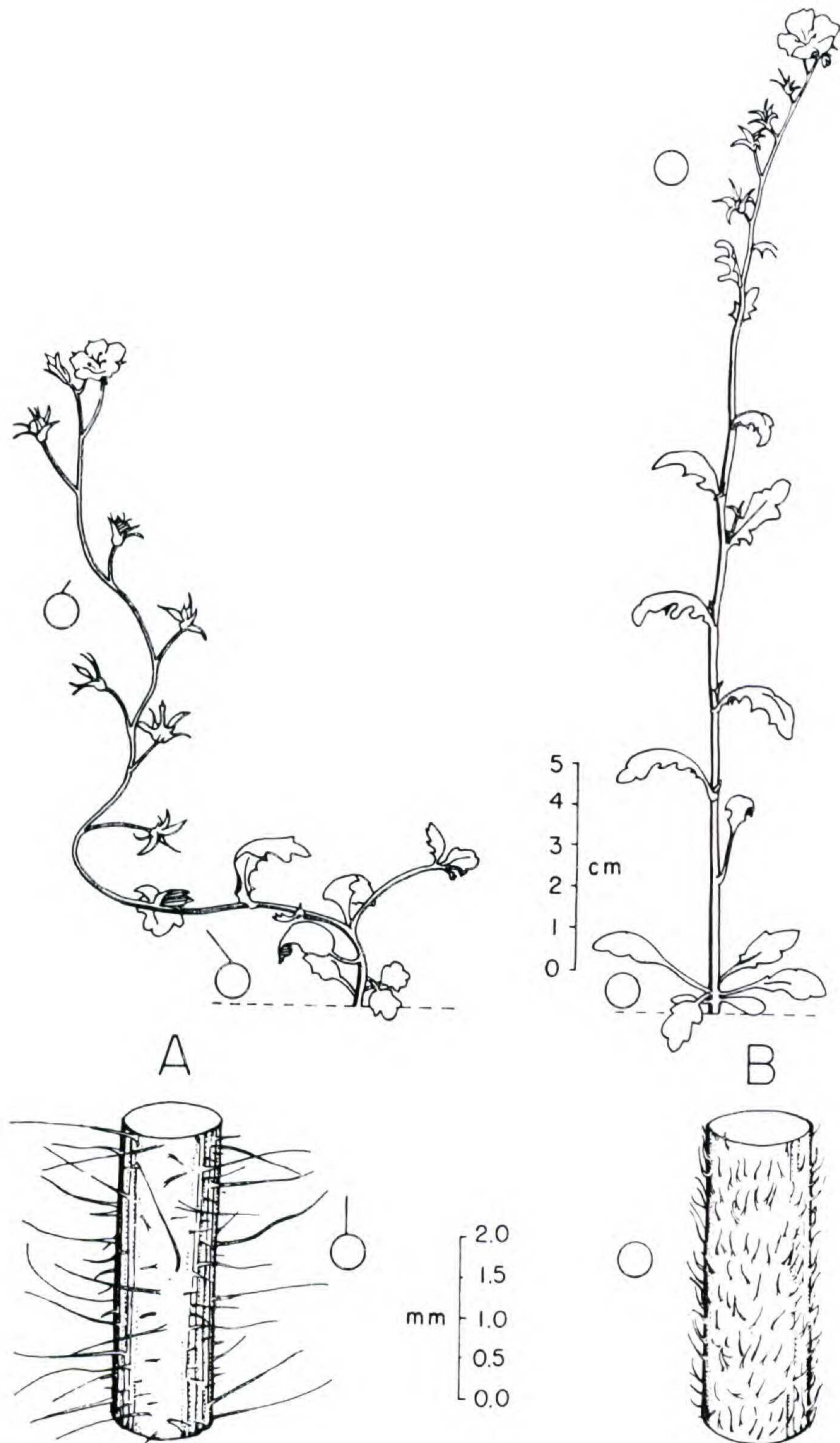


Fig. 1. Habit; pedicel length; and size and orientation of non-glandular hairs in: (A) *Phacelia patuliflora* (Gillett 1216 UC); and (B) *P. strictiflora* (Gillett 1257 UC).



A useful comparison of *Phacelia strictiflora* and *P. patuliflora* is given in the following table:

<i>Phacelia strictiflora</i>	<i>Phacelia patuliflora</i>
Corolla with crenulate to entire margin.	Corolla with entire margin.
Calyx accrescent.	Calyx non-acrescent.
Colleters small; 0.1 - 0.2 mm long.	Colleters of two size classes: small, 0.1 - 0.2 mm; and large, 0.3 - 0.5 mm long.
Habit virgate to ascending.	Habit reclining to ascending.*
Non-glandular hairs fine, ascending.	Non-glandular hairs coarse, spreading.*
Pedice! length 0.5 - 1.5 cm.	Pedice! length 1.5 - 2.0 cm.*
*Clinal variation (determined by the study of herbarium specimens).	

The variability of the last four characters in the above table was determined by direct measurement or by comparison. Voucher specimens of each species were prepared from plants grown together in the greenhouse and were used for making comparisons with herbarium specimens. Line drawings of these vouchers are shown in Fig. 1.

The glandular hairs (colleters) of *Phacelia strictiflora* and *P. patuliflora* are of two size classes that show no intergradations (Fig. 2). The larger glandular hairs are quite distinct and easily recognized on dried material, but the

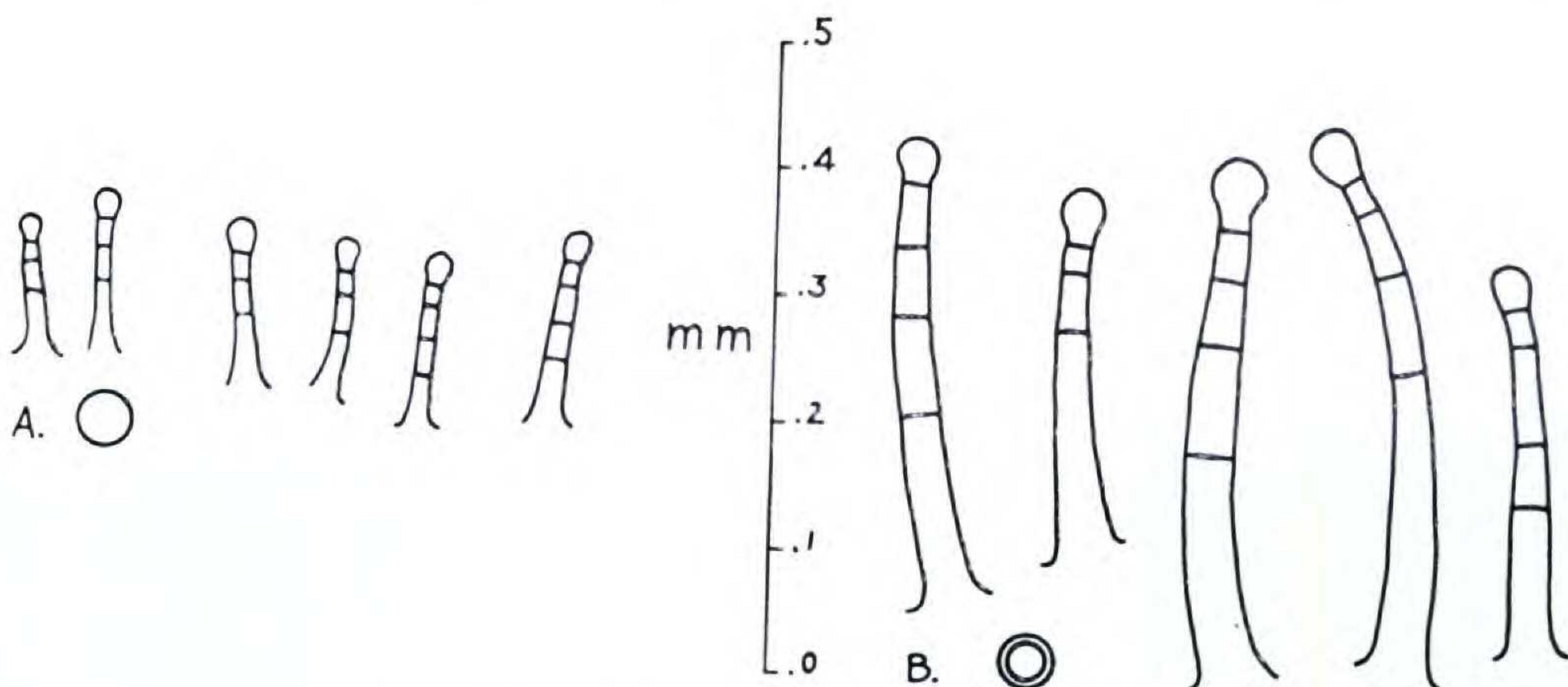


Fig. 2. Glandular hairs (colleters) of the *Phacelia strictiflora* complex. (A) small glandular hairs of *P. strictiflora* and southern populations of *P. patuliflora* (Gillett 1257 UC); (B) large glandular hairs of northern populations of *P. patuliflora* (Constance and Cory 3247 UC).



smaller become shrunken upon drying, presenting a distorted appearance. It was, therefore, quite easy to score herbarium specimens for these. The larger glandular hair is apparently restricted to the northern and interior populations of *P. patuliflora*.

The three additional characters scored in this complex were: (1) the length of the lower pedicels of the inflo-

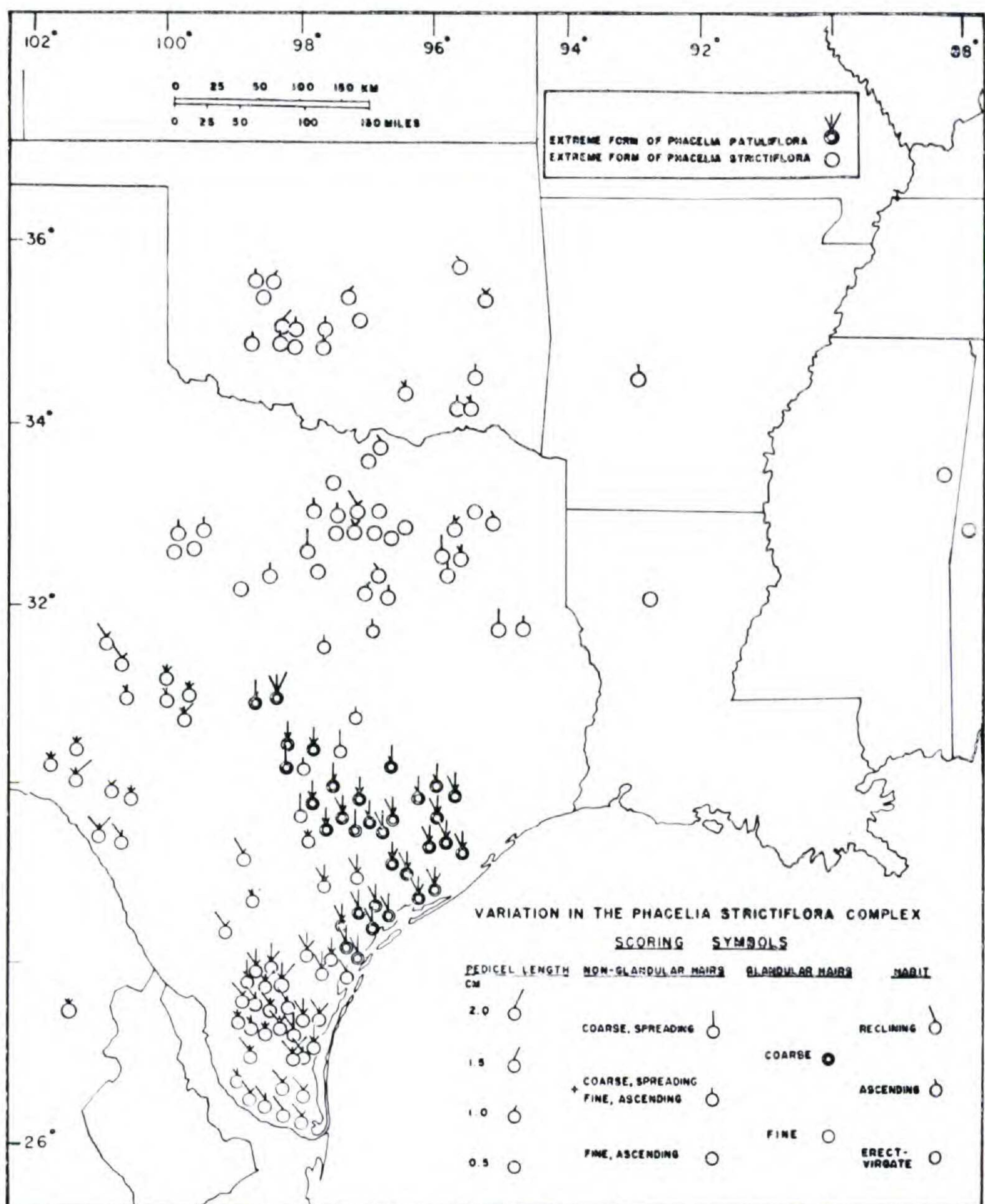


Fig. 3. Geographical distribution and variation in *Phacelia strictiflora* and *P. patuliflora*.



rescence (by direct measurement); (2) the cauline pubescence of non-glandular hairs (by comparison); and (3) habit (by comparison). Each of these three characters is metrical with a continuous spectrum of expression between the extremes portrayed in Fig. 1. The classes scored were the two extreme expressions, each with a representation of near-extremes, and an intermediate class that included an arbitrarily designated central expression along with intermediates on either side. In scoring the variation in pedicel length, two intermediate classes were designated, so that four classes were recorded for this character. The scoring for these metrical characters was admittedly unsophisticated, but it permitted a graphic portrayal of variability in each character over the entire range of the complex, so that morphological variation may be related to ecological differences. (Fig. 3).

The presence of both qualitative (glandular hairs) and quantitative characters in this material probably reflects the genetic make up of many wild plants. This genetic versatility may be even greater, for the metrical or quantitative characters could represent more than one of the four basic types of polymeric gene systems cited by Clausen & Hiesey (1958).

The four characters portrayed in Fig. 3 are correlated, so that the gene frequencies for the extreme expression of *Phacelia strictiflora* are relatively higher in the populations in Oklahoma and are progressively lower in those of central Texas, portraying generalized genoclines. On the other hand, the gene frequencies for the extreme expression of *P. patuliflora* are relatively higher in populations from central Texas (Burnet County) to the Gulf Coast and are progressively lower south to the Rio Grande. It is notable that the intermediate expression of all three metrical characters is found in widely separated populations of the southern Gulf Coast, the Edwards Plateau (about 300 miles northwest), and central Texas. The clinal variation of these characters suggests that the past migrational histories of *P. patuliflora* and *P. strictiflora* have involved contact and introgressive hybridization along the Rio Grande, or along



the northern distributional limit of *P. patuliflora*, or possibly in both regions.

It was not possible to confirm experimentally the abundant evidence of natural hybridization between *Phacelia strictiflora* and *P. patuliflora*. In the first cultures of experimental hybrids grown only two flowers of each species were cross-pollinated, with no seed resulting. In later crosses with cultures grown at Turku, Finland, seven flowers of *P. patuliflora* were pollinated with *P. strictiflora* pollen. The *P. patuliflora* stigmas were examined on the stage of a 30X stereoscopic microscope and thus verified to be clean and free of "selfed" pollen before cross-pollination. The ovules of these seven cross-pollinated flowers were analyzed between 25 and 30 days after pollination. Of 69 ovules examined, only five had normal endosperm and apparently normal embryos. The remaining 64 ovules had no visible endosperm, but 14 of these had deformed embryos. This would suggest that the sterility barrier involves failure of endosperm development and incompatibility between the embryo and surrounding tissue as discussed by Stebbins (1958) and reported in PRIMULA by Valentine (1952, 1955). In the latter work, Valentine was able to secure hybrids from over 4000 seeds obtained from his crosses. In the present material of *P. strictiflora* and *P. patuliflora*, compatibility ranges from zero to apparently normal endosperm and embryos in a very limited population of only 69 ovules. It seems most likely, therefore, that a larger number of cross-pollinations might have produced hybrids. It is also possible that additional reciprocal crosses to the *P. strictiflora* seed parent might have produced hybrids. Therefore, the incompatibility shown by these experiments appears to be relative and by no means absolute.

The taxonomic conclusions of this study provide little satisfaction in terms of readily identifiable species or varieties for the evolutionary dynamics involved here work against, rather than for, discrete taxa. Species limits are established by morphological and often geographical reference points. In *P. strictiflora* and *P. patuliflora* a broad expanse of territory contains innumerable intermediates,



each of which is a logical reference point for circumscribing the limit of either species. It is impossible to communicate a species or subspecies limit that can be unerringly confirmed by subsequent workers because a given intermediate population could be ascribed to *P. patuliflora* or to *P. strictiflora* with equal justification. Combining eco-geographical and morphological criteria, I suggest the reasonable compromise of including in *P. strictiflora* those populations of upland habitats from northeastern Mexico through the Edwards Plateau, and including those populations north of central (Burnet County) Texas. On the other hand, it seems reasonable to circumscribe within *P. patuliflora* the coastal populations and those contiguous populations extending inland to and including Burnet County, Texas. This is an admittedly imperfect designation because it leaves populations of *P. strictiflora* within the area ascribed to *P. patuliflora*, as clearly shown on the map of Fig. 3.

#### ACKNOWLEDGEMENTS

This research was carried out at the Department of Botany, University of Turku, Finland, under a Fulbright Lectureship. The space and facilities provided by Professor Antero Vaarama and his staff at Turku are gratefully acknowledged. The line drawings are by Miss Nina Tarén.

DEPARTMENT OF BOTANY, UNIVERSITY OF HAWAII

#### LITERATURE CITED

- CLAUSEN, J. and W. M. HIESEY. 1958. Experimental studies on the nature of species. IV. Genetic structure of ecological races. Carnegie Inst. Wash. Pub. 615.
- CONSTANCE, L. 1949. A revision of *Phacelia* subgenus *Cosmanthus* (Hydrophyllaceae). Contr. Gray Herb. 168: 1-48.
- GILLET, G. W. In Press. Genetic barriers in the *Cosmanthus* phacelias (Hydrophyllaceae). *Rhodora* 66: 359-368.
- STEBBINS, G. L. 1958. The inviability, weakness and sterility of interspecific hybrids. *Advances in Genetics* 9: 147-215.
- VALENTINE, D. H. 1952. Studies in British Primulas. III. Hybridization between *Primula elatior* (L.) Hill and *P. veris* L. *New Phytologist* 50: 383-398.
- . 1955. Studies in British Primulas. IV. Hybridization between *Primula vulgaris* Huds. and *P. veris* L. *New Phytologist* 54: 70-80.